

Signs of an extended and intermittent terminal spawning in the squids *Loligo vulgaris* Lamarck and *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae)

Francisco Rocha*, Angel Guerra

Instituto de Investigaciones Marinas (CSIC), C/ Eduardo Cabello 6, 36208 Vigo, Spain

*Corresponding author. Tel.: + 34 86 231930; Fax: +34 86 292762

Abstract

The reproductive pattern of *Loligo vulgaris* and *Loligo forbesi* was studied on the basis of gonad maturation, mating and spawning in males and females of both species which were present off the northwest coast of Spain (Galicia), between February 1991 and February 1993. The mature females of both species have several modes of egg sizes and developmental stages within the ovary. Several signs indicate that both female *Loligo vulgaris* and *L. forbesi* undergo partial ovulation at the time of spawning, the spawning period being relatively long, although in no case representing the greatest fraction of the animal's life before death. Egg-laying occurring in separate batches and somatic growth between egg batches has not been observed. This reproductive pattern is defined as intermittent terminal spawning. Some other terms describing different cephalopod reproductive strategies are also defined.

Keywords: *Loligo forbesi*; *Loligo vulgaris*; NW Atlantic; Reproduction; Spawning patterns

1. Introduction

Until recently, it was generally accepted that female cephalopods lay their eggs in one single spawning or in several consecutive ones, with no pause between each, after which they would die by exhaustion (McGowan, 1954; Mangold, 1987; Harman et al., 1989; Mangold et al., 1993). The animals with this reproductive pattern where gonad regeneration is absent are known as semelparous. Conversely, the iteroparous species are those in which a gonadal regeneration following spawning occurs, making new reproductive cycles possible.

As knowledge has grown regarding the biology of this group, it has become increasingly difficult to support the notion of a single reproductive pattern (Boletzky, 1981, Boletzky, 1986; Rodaniche, 1984; Harman et al., 1989; Mangold et al., 1993). A case in point is *Nautilus*, with a life span of 20 years, which must be considered as an iteroparous species since the females spawn once a year, surviving, feeding, growing and regenerating their gonads for a further reproductive event the following year (Ward, 1987). With the exception of this particular case, the other cephalopods may be considered as semelparous, although there are significant differences between the maturation processes and spawning from one species to another (Boletzky, 1975; Mangold, 1987; Mangold et al., 1993). According to these differences, several reproductive strategies may be defined in cephalopods with regard to the oocyte maturation process and to the type of spawning process in each species (Boletzky, 1981, Boletzky, 1986; Harman et al., 1989; Villanueva, 1992; Mangold et al., 1993; Gonzalez, 1994; Rocha, 1994; Rasero, 1996). The current definitions for the different reproductive cephalopod strategies are confused. For clarity and accuracy the reproductive terms used in this paper are defined.

‘Simultaneous terminal spawning’. This is a type of spawning where ovulation is synchronous, egg-laying occurs in a very short period at the end of the animal’s life before death, and there is not oocyte maturation during spawning period. Several species have been found which exhibit simultaneous terminal spawning, e.g. *Loligo opalescens*, *Illex illecebrosus* and *Todarodes pacificus* (Hixon, 1983; O’Dor, 1983; Ikeda et al., 1993). This type of spawning is also called ‘terminal spawning’ and ‘single spawning’ (Hixon, 1983; Mangold et al., 1993).

‘Intermittent terminal spawning’. In this type of spawning ‘partial ovulation’ occurs. Partial ovulation implies the presence of oocytes at various stages of development in the ovaries, thus enabling the continued production of ova once spawning has commenced. Partial ovulation has been described in several species: *Sthenoteuthis oualaniensis*, *Loligo bleekeri* and *Idiosepius pygmaeus* (Harman et al., 1989; Hun Baeg et al., 1993; Lewis and Choat, 1993). In the intermittent terminal spawning egg-laying occurs in separate batches during the spawning period which is usually relatively long, although in no case does it represent the greatest fraction of the animal’s life before death. The

species *Loligo vulgaris reynaudii* and *L. bleekeri* (Sauer and Lipinski, 1990; Hun Baeg et al., 1993) seem to be intermittent terminal spawners in which growth does not take place between separate egg batches, egg batches includes ripening of eggs and subsequent deposition. This type of spawning corresponds to ‘intermittent spawning’ defined by Boletzky (1975). A modality of the intermittent terminal spawning is the ‘multiple spawning’ (Harman et al., 1989), when somatic growth occurs between separate egg batches. Several species have been found which exhibit multiple spawning, e.g. *Octopus chierchiae*, *Sepia officinalis* and *Sthenoteuthis oualaniensis* (Rodaniche, 1984; Boletzky, 1975; Boletzky, 1987; Boletzky, 1988; Harman et al., 1989; Forsythe et al., 1991).

Another type of reproductive strategy was found in the citrate octopods *Opisthoteuthis agassizii* and *O. vossi*. This strategy is the ‘continuous spawning’, which was named and defined by Villanueva (1992).

The patterns of ovulation and spawning in *Loligo vulgaris* have received little attention. Mangold-Wirz (1963), Worms (1983), Baddy (1988), Coelho et al. (1994), Guerra and Rocha (1994), Moreno et al. (1994) and Arkhipkin (1995) described that the species has an extended spawning period, but only Guerra and Rocha (1994) have suggested that *L. vulgaris* could be an intermittent spawner. In the case of *Loligo forbesi* the evidence of an extended breeding season was also shown (Lum-Kong et al., 1992; Boyle and Ngoile, 1993; Guerra and Rocha, 1994; Moreno et al., 1994; Pierce et al., 1994; Boyle et al., 1995; Collins et al., 1995b). While Lum-Kong (1993) indicated continuous spawning for this species, Boyle et al. (1995), Guerra and Rocha (1994) and Collins et al. (1995a), (1995b) suggested intermittent spawning.

This study examines the reproductive pattern presented by both sexes of *Loligo vulgaris* and *L. forbesi* in the waters off NW Spain, thus completing the study of various aspects of the reproductive biology of both sexes of these species begun by Guerra and Rocha, 1994, particularly with regards to the duration of breeding period and types of ovulation and spawning.

2. Materials and methods

A total of 1,787 individuals of *Loligo vulgaris* were studied (862 males and 925 females), and 755 *Loligo forbesi* (399 males and 356 females), with a dorsal mantle lengths (ML) between 98 and 475 mm ML in *Loligo vulgaris* and 100 and 685 mm ML in *Loligo forbesi*. The individuals were obtained from monthly samples from commercial catches landed at ports and fishing sites in Galicia, between February 1991 and February 1993. Samples were frozen at -30°C, duly labelled and preserved for subsequent laboratory analysis. The individuals were defrosted at room temperature, their sex was determined and total weight (BW) and dorsal mantle length (ML) noted. Measurements were made in millimetres and grammes, with a margin of error of ± 0.5 mm and ± 0.01 g, respectively.

Maturity in males and females was estimated using a 5 stage maturity scale, as indicated by Boyle and Ngoile (1993). In this scale, stages IV and V represent squid in breeding condition and hence, part of the spawning stock. A gonad-somatic index (GSI) was calculated as follows:

$$GSI = \frac{GW}{BW} * 100$$

where GW is the weight of the gonad (testis or ovary).

In females the reproductive system was dissected, and the ovary (OW), the oviducal complex (oviducts, nidamental glands and accessory reproductive glands) (OCW), the proximal oviduct (POW) and the nidamental glands (NGW) were weighed separately. In males, the reproductive system was dissected, and the weights of the testis (TW) and to the spermatophoric complex (SCW) determined.

Female fecundity was estimated for mature individuals (stages IV and V), based on subsamples of ovary and proximal oviduct from the distal and medial zones weighing 0.3-1.0 g. Each sample was weighed and preserved in Gilson solution, the oocytes from the sample having been released from the surrounding tissue by brusque movements in water. The oocytes present in each ovary and oviduct subsample were counted, measuring the largest diameter using a binocular microscope with an ocular micrometer. Damaged or deformed oocytes were not measured. The size distribution of oocytes in the ovaries of both species was subjected to a size frequency distribution analysis using the method of Bhattacharya (1967) to check for the presence of different size groups.

The Bhattacharya method, as implemented in the ELEFAN software (Gayanilo et al., 1989) was used to identify putative size groups within size distribution of oocytes in each ovary. The method assumes that the size of oocytes within each size group is normally distributed. An interactive routine is used to define the component size groups, with goodness of fit assessed by χ^2 tests.

The spermatophoric complex from mature males (stages IV and V) of different sizes was labeled and preserved in formalin (5%). A subsample of each complex was weighed, counting the spermatophores which they contained and measuring the spermatophore length (SL). Deteriorated spermatophores were excluded from the measuring. In each case, the total number of spermatophores (SN) was estimated from the measured subsample.

3. Results

In mature male and female of *Loligo vulgaris* and *L. forbesi* a large variation in the GSI/ML ratio was found (Fig. 1). In both species and sexes, the GSI decreased with the increasing in ML.

In stage V male *Loligo vulgaris*, a large variation in the SCW/BW ratio was observed relative to ML (Fig. 2a). Individuals below 380 mm ML had GSI greater than 1.3%, whereas larger squid has GSI less than 1.3% (Fig. 2a). There was also a large variation between the SL and the SCW/BW (Fig. 2b). It was observed, however, that individuals with a GSI above 1.3% had smaller spermatophores than those with a GSI below 1.3% (Fig. 2b). Between specimens of a range of SL (13-17 mm), those with a GSI above 1.3% showed larger spermatophoric complexes.

In stage V male *Loligo forbesi*, a gradual decrease in the SCW/BW ratio was found, relative to the ML (Fig. 3a). Males with a GSI of over 1.3% were present at sizes below 410 mm ML, whereas those with a GSI below 1.3% had sizes above 410 mm ML and smaller spermatophoric complexes (Fig. 3a). The SCW also decreased with the SL (Fig. 3b). It was noted that male *L. forbesi* with a GSI above 1.3% presented a larger complex and smaller sized spermatophores than the males with a GSI below 1.3% (Fig. 3b).

The diameter of oocytes in *Loligo vulgaris* ovaries varied between 0.1 and 4.1 mm, whereas in female *L. forbesi*, the range was between 0.1 and 4.3 mm. In both species, the mature female ovaries of all the sizes studied showed slightly different polymodal distributions of oocytes, depending on the individual examined (Fig. 4). Because the distribution of diameters in oocytes in each ovary varies from individual to individual within the same species, mean sizes and the standard deviations for each species are plotted as shown in Fig. 5. Analysis of size distribution of oocytes in the ovaries of 9 female *L. vulgaris* showed the presence of 3 to 5 modal groups of oocytes, depending on the individual studied. A minimum of 3 and a maximum of 7 modal size groups of oocytes were found in the ovaries of 14 mature female *L. forbesi* (Table 1).

The mean size of oocytes in the proximal oviduct of *L. vulgaris* (2.74 mm; SD = 1.54 mm) and *L. forbesi* (3.06 mm; SD=0.28 mm) is indicated in Fig. 5. The number of oocytes in the proximal oviduct of mature females in both species varied directly with ML (Fig. 6). In *L. vulgaris*, the maximum number of oocytes present was 10,000, whereas in *L. forbesi*, the number rose to 4,700.

Nidamental gland weight (NGW) increased with size in females of both species (Fig. 7). In the case of females with GSI below 4.0, however, this weight was less than that for females of the same size, with an average GSI of between 4.0 and 7.0, or of over 7.0. This relationship was exponential in each case (Table 2).

4. Discussion

The presence of small (ML<380 mm) mature male *Loligo vulgaris* with small spermatophores, GSI > 1.3, and highly variable SCW/BW ratio, together with large mature male *L. vulgaris* with big spermatophores, GSI < 1.3, and the same variability in SCW/BW ratio that formers, could be explained in two different ways: 1) Spermatophores may be produced throughout the prolonged mating period resulting in depletion of the testis. Since the SL/ML ratio is linear (Guerra and Rocha, 1994), the length of the spermatophores increased in the same given mature animal while it is growing somatically. 2) The existence of two groups of squid at maturity, the younger and smaller ones having relatively large gonads, the large older ones having smaller gonads, but larger spermatophores. If large maturity size is achieved at the expense of

reproductive investment, then one might expect to see the smaller GSI in the larger mature squid. These two groups of squid at maturity found in the species by Coelho et al. (1994) and Guerra and Rocha (1994) seems to be represented by animals of different ages (Rocha, 1994; Rocha and Guerra, in prep.).

In stage V male *Loligo forbesi* of maturity, SCW/BW varied among individuals of the same ML, gradually decreasing as ML increased. GSI also decreased when ML increased. The existence of two size groups of squid at maturity (Guerra and Rocha, 1994; Boyle et al., 1995; Collins et al., 1995a) is a better argument than somatic growth during mating to explain the reproductive pattern found in males of this species because the gradual decrease in SCW/BW vs ML relationship (Fig. 3). On the contrary that in *L. vulgaris*, these two groups of *L. forbesi* at maturity seems to be represented by animals of similar ages, although further ageing analysis are necessities (Rocha, 1994; Boyle et al., 1995; Rocha and Guerra, in prep.).

The discrepancy between the size categories of the oocytes in the ovaries of both species noted in Guerra and Rocha (1994) and the ones presented here is due to that the size distribution of oocytes in the ovaries has been analysed more accurately, avoiding the previous imprecise clasification into three categories (large, medium and small oocytes).

The presence of an asynchroneous development in loliginid oocytes was histologically shown in *Loligo vulgaris reynaudii* (Sauer and Lipinski, 1990) and in *L. bleekeri* (Hun Baeg et al., 1993), and it suggest that both species spawn intermittently.

The size distribution of ovarian oocytes in *Loligo forbesi* at different stage of maturity shown by Lum-Kong (1993) led her to suggest that spawning is continous in that species. But, from our view, Lum-Kong's data are not sufficient to support that continous spawning is occurring in *L. forbesi*. When the oocyte distribution of more than one specimen is added and then analysed, as was done by this author (compare Fig 4 and Fig. 5), the presence of dominant size modes vanish. Moreover, the mere presence of oocytes at different stages of maturity during the spawning process is insufficient to identified any species as multiple spawning (Mangold et al., 1993). This because multiple spawning implies that somatic growth occurs between separate egg batches

(Harman et al., 1989), which was not observed in the case of *Loligo vulgaris* and *L. forbesi*.

These two loliginid squid may not be either considered as simultaneous terminal spawners. In a simultaneous terminal spawning species, the majority of oocyte production must be available for egg-laying within a very brief period of time (Jackson and Mladenov, 1994); this occurs in *Loligo opalescens* (McGowan, 1954; Knipe and Beeman, 1978), but in *L. vulgaris* and *L. forbesi*, this is very improbable due to the fact that all the oocytes do not mature at the same time (partial ovulation), and that the oviduct would be unable to manage the entire production all at once.

There are also several signs in *Loligo vulgaris* and *L. forbesi* which support the existence of multiple spawning in *Sthenoteuthis oualaniensis* (Harman et al., 1989), but they are not, however, clear evidences of multiple spawning nor of intermittent spawning. These signs are: (a) the wide variation in the total number of oocytes in the oviduct and ovary in females at the same stage of maturity and of the same ML. This might also be explained, however, by a variable growth rate, which is well documented in both loliginid species (Natsukari and Komine, 1992; Guerra and Rocha, 1994; Arkhipkin, 1995; Collins et al., 1995c), where some females might be expected to mature earlier than others; (b) the wide ML range covered by stages IV and V of maturity in *Loligo vulgaris* and *L. forbesi* (Guerra and Rocha, 1994). Again, this point may be similarly explained by the fact that there is reasonable evidence for two size modes of mature males and females in both species (Coelho et al., 1994; Guerra and Rocha, 1994; Boyle et al., 1995; Collins et al., 1995a).

The decrease of the NGW and GSI respect to ML observed (Fig. 7) could be explained as a fall in the NGW after a spawning event. It remains to be seen, however, whether nidamental gland weight would decrease in females which have spawned on one or more than one occasion prior to being caught.

In conclusion, evidence strongly supports extended and intermittent terminal spawning in *Loligo vulgaris* and *L. forbesi*, as suggested by Guerra and Rocha (1994), Collins et al. (1995a) and Boyle et al. (1995) although evidence for multiple spawning is minimal.

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Fig. 1. Relationship between the dorsal mantle length (ML) and the gonad-somatic index (GSI) in mature male and female of *Loligo vulgaris* (A and B) and *Loligo forbesi* (C and D), respectively.

Fig. 2. Relationship between the dorsal mantle length (ML) and the ratio spermatophoric complex weight (SCW)/Body Weight (BW) (A) and between spermatophore length (SL) and the SCW/BW (B) in male *Loligo vulgaris* at stage V of maturity. ▲, GSI above 1.3%; □, GSI of below 1.3%.

Fig. 3. Relationship between the dorsal mantle length (ML) and the ratio spermatophoric complex weight (SCW)/Body Weight (BW) (A) and between spermatophore length (SL) and SCW/BW (B) in male *Loligo forbesi* at stage V of maturity. ▲, GSI above 1.3%; □, GSI of below 1.3%.

Fig. 4. Frequency distribution of oocytes in the ovary of three individuals of *Loligo vulgaris* (A) and *Loligo forbesi* (B), with to size intervals of 0.2 mm (in the figure, the upper limit of the interval is shown). ML: Dorsal Mantle Length.

Fig. 5. Average distribution of diameters of oocytes and standard deviation in the ovary of mature *Loligo vulgaris* (A) and *Loligo forbesi* (B) females, with size intervals of 0.2 mm (in the figure, the upper limit of the interval is shown). N: Number of ovaries examined; Arrow: Mean size of oocytes in proximal oviduct.

Fig. 6. Relationship between the dorsal mantle length (ML) and the number of oocytes present in the proximal oviduct of *Loligo vulgaris* (A) and *Loligo forbesi* (B).

Fig 7. Relationship between the dorsal mantle length (ML) and nidamental gland weight (NGW) in mature female *Loligo vulgaris* (A) and *Loligo forbesi* (B), according to their GSI. ▲, $GSI \geq 7.0$ (1); ■, $4.0 \leq GSI < 7.0$ (2); □, $GSI < 4.0$ (3).

Table 1
Number of oocyte modal size groups found in ovaries of *Loligo vulgaris* and *Loligo forbesi* by polymodal analysis

Modal sizes	Loligo vulgaris Percentage	Loligo forbesi Percentage
3	44.5	7.1
4	33.3	42.9
5	22.2	35.8
6	-	7.1
7	-	7.1
Number	9	14

Table 2

The relationship between the nidamental gland weight (NGW) and dorsal mantle length (ML) in mature female *Loligo vulgaris* and *Loligo forbesi*, according to the Gonadosomatic index (GSI)

	a	b	r ²	N
<i>Loligo vulgaris</i>				
GSI ≥ 7.0	0.0000062	2.699	0.77	22
4.0 ≤ GSI < 7.0	0.0001151	2.134	0.83	49
GSI < 4.0	0.0002112	1.985	0.56	18
<i>Loligo forbesi</i>				
GSI ≥ 7.0	0.0000228	2.488	0.88	7
4.0 ≤ GSI < 7.0	0.0000719	2.238	0.67	23
GSI < 4.0	0.0000004	3.117	0.86	9

Equation: $W = aL^b$; r²: determination coefficient; N: number of individuals.